Dominance-related contributions to collective territory defence are adjusted according to the threat

Jenny E. York*[1,2] Katrina J. Wells[1] Andrew J. Young[1]

[1]Centre for Ecology & Conservation, University of Exeter, Penryn Campus, Penryn, U.K.

[2]Department of Zoology, University of Cambridge, Cambridge, U.K.

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*Correspondence: J. E. York, Department of Zoology, Downing Street, University of Cambridge, Cambridge CB2 3EJ, U.K.

E-mail address: jenny.e.york@gmail.com

Across diverse societies, group members benefit from the cooperative maintenance of a shared territory (a public good). How such public goods are maintained has received extensive interest, yet individual contributions to cooperative territory defence remain poorly understood. Recent theory predicts that, in groups with social hierarchies, privileged individuals will contribute most to competition with rival groups as they benefit most from defence of the territory. Here, we investigated whether dominant individuals contribute more to territory defence in a group-territorial bird in which dominants monopolize within-group reproduction: the white-browed sparrow-weaver, *Plocepasser mahali*. Using simulated territorial intrusions, we demonstrate that dominants contributed significantly more than subordinates to territory defence. We also found that individual contributions were adjusted

according to threat: males of both social classes significantly and similarly increased their contributions to defence in response to a high threat (playback of an unfamiliar pair's duet, rather than that of a neighbouring pair), which was associated with a stronger collective response by the group. Thus, while dominants contributed most as predicted by the asymmetry in benefits, subordinates did increase contributions when they were needed most (in small groups and under greater threat). Contributions by subordinates when needed most also highlights that dominants could still benefit substantially from tolerating the presence of subordinates despite their overall lower contributions. Our results show that public goods can be maintained despite unequal contributions and highlight the potential importance of context-dependent behavioural flexibility in mitigating collective action problems.

Keywords: animal societies, collective action problem, cooperation, free riding, free-rider problem, individual contributions, social evolution, territory defence, behavioural flexibility, plasticity

In human societies, individual contributions to public goods (a benefit available to all group members) are often a legal or moral requirement enforced by punishment, yet in animal societies, evidence of punishment is relatively rare (Arseneau-Robar et al., 2018; Bshary & Bshary, 2010; Clutton-Brock & Parker, 1995; Fehr & Fischbacher, 2004; Heinsohn & Packer, 1995; Johnson, 2005; Raihani, Grutter, & Bshary, 2010; Raihani, Thornton, & Bshary, 2012; Riehl & Frederickson, 2016; Sigmund, et al., 2010; West & Gardner, 2004). What mechanism stabilizes cooperative contributions to public goods sufficiently for collective action (and the resulting public good) to persist despite selection for free riding (cheating) in animal societies has been much debated (Dugatkin, 1997; Nunn, 2000; Nunn & Lewis, 2001; Raihani et al., 2012; Riehl & Frederickson, 2016). Olson (1965, page 35) suggested that high-

status individuals will contribute the most, while lower status individuals gain benefits without paying the full cost: 'the exploitation of the great by the small'. More recently, theoretical models (Gavrilets & Fortunato, 2014) have been developed that formalize the prediction that dominant individuals should contribute more to the maintenance of public goods while subordinates should be more likely to free-ride, because the dominant individuals benefit disproportionately more from the maintenance of the public good. Indeed, in many animal societies socially dominant individuals do stand to reap greater benefits from the maintenance of public goods, such as a shared territory, as they often breed at substantially higher rates than their subordinates (Hager & Jones, 2009; Keller & Reeve, 1994). However, the role that social dominance plays in governing individual variation in contributions to public goods in animal societies has received little empirical attention (Heinsohn & Packer, 1995; Mares, Young, & Clutton-Brock, 2012; Nunn, 2000).

Group territory defence provides an opportunity for testing theoretical predictions about the role of within-group social dominance in determining individual contributions to public goods (Heinsohn & Packer, 1995; Mares et al., 2011; Mares et al., 2012). Territory defence is widespread across group-living species, and while all individuals may benefit from contributing to maintenance of the shared territory (access to resources, safety from predators and more efficient foraging; Ridley et al., 2008), dominant individuals frequently monopolize the reproductive opportunities (Hager & Jones, 2009; Keller & Reeve, 1994). Contributions to territory defence are also likely to entail costs (energy, time), including a risk of harm to oneself via physical injury or even fatality (Heinsohn & Packer, 1995; Mares et al., 2012; van Schaik, 1996), leading to the prediction that subordinates should withhold risky contributions given their lower expected benefits from the maintenance of the public good (Gavrilets & Fortunato, 2014). Indeed, studies of a number of species have reported dominance-related differences in contributions to territorial defence, including ring-tailed lemurs, *Lemur catta*,

63 and several other primate species (Cords, 2007; Kitchen & Beehner, 2007; Nunn & Deaner,
64 2012), lions, *Panthera leo* (Heinsohn & Packer, 1995) and feral domestic dogs, *Canis lupus*
65 *familiaris* (Bonanni, Valsecchi, & Natoli, 2010). Furthermore, individual contributions are
66 negatively associated with group size in capuchins, *Cebus capucinus* (Crofoot & Gilby, 2012)
67 and feral domestic dogs (Bonanni et al., 2010), lending some empirical support to the
68 prediction that low-rank individuals should be more likely to withhold contributions when in
69 larger groups (Gavrilets & Fortunato, 2014; Olson, 1965).
70
71 It has long been suggested that the cooperative contributions of subordinate group members
72 to territory defence may have played a role in selection for dominants to tolerate the presence
73 of subordinates, and hence for group living to evolve (Ekman & Griesser, 2002; Riehl &
74 Frederickson, 2016; Woolfenden & Fitzpatrick, 1978; potentially acting in concert with other
75 benefits of grouping; Griesser et al 2017). However, if socially dominant individuals
76 contribute most heavily to the maintenance of public goods while their subordinates
77 contribute little, this has the potential to undermine the utility to dominants of tolerating the
78 presence of subordinates on the territory, given the potential costs of sharing resources
79 (Ekman & Griesser, 2002; Woolfenden & Fitzpatrick, 1978). One potential mechanism that
80 could resolve this problem is if subordinate individuals adjust their contributions to territory
81 defence according to the level of threat to the shared territory, investing more when the threat
82 is greatest. Few studies have examined whether individual contributions are adjusted
83 according to the scale of the threat (Heinsohn & Packer, 1995), but evidence that individuals
84 are more likely to contribute when in smaller groups could be interpreted as investment in
85 cooperative contributions when they are most needed to defend the shared resource (Bonanni
86 et al., 2010; Crofoot & Gilby, 2012).
87

Here, we investigated the role of social status and the level of threat in governing individual contributions to territorial defence in cooperatively breeding white-browed sparrow-weavers, *Plocepasser mahali mahali*. This species is a year-round territorial, cooperatively breeding passerine that is common throughout sub-Saharan Africa (Harrison, York, & Young, 2014; York, Young, & Radford, 2014). They live in groups of 2–12 individuals in which a single dominant pair monopolize within-group reproduction and subordinates of both sexes contribute to a range of cooperative activities including territory defence (Collias & Collias, 1978; Harrison, et al., 2013a; Harrison, et al., 2013b; Walker, York, & Young, 2016). Groups aggressively defend their territory from intrusions by individuals, pairs and neighbouring groups using duets (the dominant pair) or vocal choruses (typically the dominant pair plus at least one other group mate) that will then escalate to chasing and physical aggression (Lewis, 1982; Walker, York et al., 2016; Wingfield, Hegner, & Lewis, 1992; York, 2012). Typical group territorial behaviours exhibited by white-browed sparrow-weavers during interactions between a resident group and one or more individuals from outside the group include rapid movement up to a vantage point and gathering in close proximity to other members of the group, followed by loud duet or chorusing vocalizations by at least two of the assembled resident group members at any one time (Collias & Collias, 1978; Collias & Collias, 2004). Previous studies of a more northerly subspecies, *P. m. pectoralis*, suggest that dominant individuals may indeed play a larger role in territory defence than their subordinates (Wingfield et al., 1992; Wingfield & Lewis, 1993), but the cooperative contributions of subordinates and their context dependence have yet to be investigated directly.

Specifically, we addressed two main questions: (1) does social status predict individual contributions to group territory defence in accordance with individual dominance-related payoffs from contributions (i.e. do dominant individuals contribute more than subordinates)

and (2) when faced with territory intrusions that differ in threat level, do subordinate individuals positively adjust their contributions (i.e. increase their contributions when the threat level is higher)? To address this second aim, we exploited variation in intruder threat level known as the 'dear-enemy' effect (Christensen & Radford, 2018; Temeles, 1994). Territory residents are frequently less responsive to intrusions by neighbouring territory holders than they are to unfamiliar intruders, a pattern that is thought to arise in part because unfamiliar intruders represent a greater territory threat to residents than do established residential neighbours. Based on this, we carried out a paired within-individual repeated measures playback experiment with two threat level treatments: a 'low-threat' neighbouring pair duet and a high-threat' non-neighbouring pair duet. We predicted that, given the differential reproductive payoff of defending their territory, dominant individuals would show greater individual contributions than subordinates. We also predicted that, while subordinates would contribute less than dominants, they should increase their cooperative contributions under simulated intrusion by non-neighbours, which may represent a greater threat of territory takeover. If subordinates do increase their contributions when they are needed most, individual subordinates may also be more likely to contribute to the collective territorial response to intrusions when their group size is small (Crofoot & Gilby, 2012; Gavrilets & Fortunato, 2014; Olson, 1965), and so we also exploited natural variation in the size of the focal resident groups in our data to investigate this prediction.

Methods

General methods

Data were collected between September–October 2012 and March–April 2013 from a colour-ringed population of cooperatively breeding white-browed sparrow-weavers in an area of approximately 1.5 km^2 at Tswalu Kalahari Reserve (27°16'S, 22°25'E), South Africa

(Harrison et al., 2014; York et al., 2014). All birds were fitted with a single metal ring and three colour rings for individual identification, under SAFRING licence 1444, and were semihabituated to observation (Walker et al., 2016). The study population forms a single contiguous block of adjoining territories of 30–40 groups that have been monitored since 2007. Group composition information (number and identity of individuals) was determined by weekly monitoring observation sessions and targeted captures of the group. The dominant bird of each sex was determined by weekly monitoring of dominance-related aggressive, displacement and reproductive behaviours (Harrison et al., 2013; York, et al., 2016). Adult males and females can be readily distinguished from about 6 months of age as males have black beaks while females have paler pinkish beaks (Harrison et al., 2014). Group size was determined using group composition data from routine weekly monitoring and confirmed at the time of data collection for each simulated territory intrusion (see below). None of the groups were actively breeding (laying, incubating, provisioning nestlings) at the time of the stimulated intrusions or playback trials (based on routine monitoring (Harrison et al., 2014) and confirmation on the week of the trial). The study comprised two discrete data collection approaches: in the first we characterized status-related differences in individual contributions using intrusions by unfamiliar pairs, that is, 'standardized simulated territorial intrusions', and in the second we experimentally manipulated the perceived threat level posed by the simulated intrusion 'threat level experiment' (York, 2019).

Standardized simulated territorial intrusions

Natural intergroup interactions are unpredictable, relatively infrequent and occur rapidly, making them challenging to study. Therefore, to collect standard data on individual contributions to territory defence, we performed simulated territorial intrusions (STIs) at group territories ($N = 27$) using a portable loudspeaker (Jawbone, Jambox) placed at a height of 1.5 m on the main sleeping roost tree on the focal group's territory (to represent a maximal

threat to the resident group), with the speaker oriented in the direction of the foraging social group. The aim of these STIs was to assess dominance-related differences in individual contributions to a standard intrusion. The duet of a non-neighbouring pair was broadcast by triggering a playback track when all members of the group were foraging on the ground within approximately 10 m of the loudspeaker. Some groups were challenged with an STI more than once, to obtain some estimates of individual consistency in contributions towards STIs (see Results).

Playback stimuli

The playback audio tracks were produced using CoolEditPro 2.0 (Syntrillium Software Corporation, Phoenix, AZ, U.S.A.) from natural duet recordings ($N = 13$), each given by a resident dominant pair in response to a standard duet playback (recorded from a dominant pair in a non-neighbouring group) at a distance of approximately 10 m using a Sennheiser ME66 directional microphone with a K6 power module (2004 Sennheiser) and a Marantz PMD660 solid-state recorder (D and M Holdings Inc., Kawasaki, Japan) in 48 kHz, 32-bit WAV file format. We used playback to collect these recordings to ensure that (1) the duet stimuli recorded for this study were all produced under a standardized social context, and (2) all playback stimuli used in this study represent duets given in an interactive context. The recordings collected from pairs duetting in response to playback as described above were then used to create the stimulus playback tracks as follows. Each playback track was 3 min long, consisting of eight repetitions of a natural duet at 20 s intervals (typical production rate during encounters). Playback tracks were broadcast at an amplitude of 85 dBA (at 1 m), which is comparable to natural duets which were measured (using a Voltcraft SL100 digital sound level meter, Voltcraft, Barking, U.K.) at an average of 65 dBA at 10 m (based on the inverse square law of sound intensity reduction over distance).

Behavioural responses to STIs

Observational data (168 observations of 122 birds during 39 STIs at 27 social groups) were dictated and recorded on a DM550 Olympus recorder (ME15 Olympus microphone) by one observer (J.Y.) during the 3 min simulated intrusion, while continuously observing the social group using a field scope. In response to simulated intrusion, invariably two or more of the terrestrially foraging social group moved to an elevated position, close to one another, became vigilant and began a vocal response. Two response metrics were derived for each simulated intrusion based on individual behaviours: (1) the identities of the individuals that contributed to the first response (those that immediately moved to an elevated position, close to other responding group mates and began a duet or chorus vocal response lasting 2–8 s); (2) the identities of the individuals that contributed at all during the trial: those that contributed during the first response plus those individuals that subsequently joined the response (i.e. moved close to the group members involved in the first response) at any subsequent point during the remaining 3 min period of the simulated intrusion, as further duets or choruses were produced by the assembled individuals, but the remaining group mates (if any; 'noncontributors') continued to forage on the ground. There were four cases where it was unknown whether specific individuals contributed during the first response by the group (as not all group members could be identified confidently due to the dynamic nature of the response in this large group); therefore, these missing observations did not contribute to the behavioural response data set (168/172 observations were used in analyses), but these individual birds were nevertheless present during the STI and therefore contributed to determining the overall group size for the two individuals confidently identified to be contributing. Throughout the trials, any acts of intragroup aggression that could be deemed as 'punishment' (a bird chased off the territory, displaced from a foraging or perching location, pecked at, other physical aggression or full fights where one individual pins another

213 individual to the floor and aggressively pecks the other; Collias & Collias, 1978; Harrison et
214 al., 2014) were actively searched for in the observations.
215
216 **Threat level experiment**
217 We carried out a paired within-individual repeated measures design experiment to investigate
218 whether individual contributions to territorial defence are adjusted in response to the level of
219 threat experienced. We focused this experiment on males because our initial results in
220 response to STIs (see below) highlighted no sex difference in contributions; therefore, it is
221 reasonable to expect that males' responses in this experiment would be representative of both
222 sexes, and logistical constraints meant that it was not feasible to monitor both males and
223 females. Each focal group contained one or more subordinate males and a dominant male,
224 and where more than one subordinate male was present, the oldest was selected for focal
225 observations along with the dominant male. Focal groups were selected based on having a
226 neighbouring group that was a pair with no subordinates, so that the simulated intrusion of
227 this pair would be naturalistic, and because an intrusion by an unfamiliar pair represents the
228 founding or annexing of territory by a pair forming a new group. The size of the focal groups
229 was three to five individuals, which provided a manageable number of individuals to track
230 during observations, and increased the probability of our being able to measure contributions
231 by subordinates (given that the probability of subordinates contributing declines with
232 increasing group size; Fig. 1). Immediately prior to each experiment, we verified that all
233 group members were present as expected based on routine monitoring as described above.
234
235 At each focal group ($N = 12$), a loudspeaker was placed at a height of 1.5 m in a tree at least
236 20 m from the focal group's main roost tree, in the direction of a neighbouring group's
237 territory and the same position was marked and used for both of the treatments conducted at

each focal group. Playbacks were broadcast by remotely triggering a playback track 10 m from the group, when all members of the group were foraging on the ground within approximately 10 m of the loudspeaker. Presentation order of the threat level treatments was alternated across groups (to balance for order of presentation effects) and the two treatments were presented on consecutive days (to reduce any influence of changes in within-group dynamics or environmental conditions), and at the same time of day for a given focal group. All trials were carried out between 0600 and 1100 hours.

Playback stimuli

The playback audio tracks for the threat level experiment were all created using recordings from natural pairs (i.e. 'dominant' pairs that lacked subordinate group members). For the experiment, each focal group that was to receive playbacks was assigned a 'neighbour' (low threat) playback track and a 'non-neighbour' (high threat) playback track. The 'neighbour' playback stimuli were recorded from the focal group's neighbouring pair. The 'non-neighbour' playback stimuli were selected for a focal group based on (1) the distance between the groups (at least three territories away) and (2) ensuring that no focal group member was likely to have had sustained contact with either individual of the pair from which the recording was made (based on known periods of group membership in all of the groups concerned). Playback stimuli were created as described above, except that in this experiment each stimulus track consisted of the sequence of the first five natural duet phrases produced by the source pair when responding to an unfamiliar duet playback, to maintain identifying information in the natural sequence from that pair. Playback stimuli were broadcast at a standardized amplitude (as above).

Behavioural responses

Observational data were collected by dictation by two observers (J.Y. and K.W.) during the playback trial. Each observer followed one predetermined individual male, either the dominant male or the oldest male subordinate in the group. For a given focal group, the two observers followed the same individual for both playback treatments, but between focal groups the observers alternated whether they followed the dominant or the subordinate individual, to avoid observer bias. The focal males were observed throughout the 3 min trial and until 8 min had elapsed since the trial was initiated (by which point the majority of individuals had ceased showing territorial behaviour and returned to foraging). Four response measures were recorded for each trial. We recorded two measures of individual male contribution to territory defence: (1) the latency to first movement response by the focal male (moving up to an elevated position having ceased foraging on the ground, immediately followed by vocal contributions) and (2) the latency to resume foraging after the onset of the playback trial. We also recorded two measures of overall group level response to the territorial intrusion, to confirm the predicted stronger overall response to the higher threat stimuli: (3) the proportion of the group that contributed to the first chorus by the group and (4) the duration of the first chorus by the group (where more than three individuals contributed to the vocal response; Collias & Collias, 2004). If more than half of the contributions to the first chorus could not be confidently attributed to individual group members, the trial was abandoned (no data were used from this attempt in the analyses), and the group was revisited for both treatments a week later. Throughout the trials, we noted any acts of intragroup aggression that could constitute 'punishment' (a bird chased off the territory, displaced from a foraging or perching location, pecked at, other physical aggression or full fights where one individual pins another individual to the floor and aggressively pecks the other; Collias & Collias, 1978; Harrison et al., 2014).

288 **Statistical analysis**

289 All analyses were conducted in R 3.2.5 (R Development Core Team, 2015). We fitted mixed-
290 effects models (Bates, Maechler, & Bolker, 2014) including all terms of interest (full model).
291 The significance of each explanatory variable was then determined by testing for the change
292 in deviance in the fit of the model when that specific term was removed from the full model,
293 unless otherwise stated below (Forstmeier & Schielzeth, 2011). Model assumptions were
294 checked and, where appropriate, met the assumptions of normality of residuals, and did not
295 show unacceptable levels of overdispersion, zero inflation and heteroscedasticity unless
296 otherwise stated (R package 'DHARMa'; Hartig, 2016).

297

298 ***<H3>Standardized simulated territorial intrusions***

299 Two generalized linear mixed-effects models (GLMMs) with binomial error (logit-link
300 function) were used to analyse individual contributions to territory defence in response to
301 standard STIs. The following terms were specified in both models: social status (subordinate
302 or dominant), sex (male or female) and group size (total number of birds in the group at that
303 time) and the status*group size interaction. In model 1, the binary response term was
304 'contributed to first response: Yes/No', and in model 2 the binary response term was
305 'contributed at all during trial: Yes/No'. Both models contained multiple observations of
306 particular individuals and observations of multiple individuals from the same social group, so
307 'bird ID' and 'social group' were both fitted as random terms. The random term 'social
308 group' was dropped from both the full models to avoid unreliable effect estimates caused by
309 model convergence failure when the term was included alongside the fixed effect of 'group
310 size'. In both cases, removing this random term caused negligible reduction in explanatory
311 power ($P = 0.99$); therefore, exclusion of the term was deemed justified in producing a more
312 robust model.

313

314 ***Threat level experiment***

315 Analysing the effects of social status and threat level on individual contributions to territorial
316 responses required an analytical approach that can cope with censored data (a continuous
317 response term 'capped' at one or both ends of the distribution due to the sampling method).
318 Specifically, while the two latency variables (latency to first response and latency to return to
319 foraging) typically contained absolute values below the total observation time, in some cases
320 the focal event had not occurred by the end of the observation period, necessitating the use of
321 an analytical approach that can use both the latency information contained in these 'censored'
322 events and the shorter absolute latency values typically obtained. Mixed-effects survival
323 models (MESM) with Cox proportional hazards (Therneau, 2015; package 'Coxme') were
324 used because they can cope with this type of censored data and random terms can be fitted.
325 One model was used for each response term 'latency to first response' and 'latency to return
326 to foraging'. In both cases, the fixed terms were 'treatment' (neighbour or non-neighbour
327 playback stimulus) and 'social status' (subordinate or dominant) and the 'treatment*social
328 status' interaction. The random terms 'bird ID' and 'group ID' were included to account for
329 repeated measures from the same individuals and social groups. To test for the effects of the
330 terms 'social status' and 'treatment', the 'treatment*social status' interaction was necessarily
331 first removed from the full model.

332

333 To analyse group level responses to the two experimental treatments two additional analyses
334 were performed. A GLMM with a binomial error structure was used to investigate whether
335 the proportion of group members that responded during the first vocal chorus response to the
336 playback was predicted by treatment. The response term was the number of birds that did and
337 the number of birds that did not respond during the first group response, with 'group ID'

included as a random term to account for repeated measures. A linear mixed-effects model (LMM) with normal error distribution was used to investigate whether the duration (s) of the first vocal chorus produced by the group during the first response to the playback was predicted by treatment (neighbour, non-neighbour), with 'group ID' included as a random term.

Results

Responses to simulated intrusions were qualitatively similar to responses to natural intrusions or interactions with individuals from other social groups. Typical group territorial behaviours of white-browed sparrow-weavers during interactions between a resident group and one or more individuals from outside the group included rapid movement up to a vantage point and gathering into close proximity to other members of the group, followed by loud duet or chorusing vocalizations by at least two of the assembled resident group members at any one time, as previously described (Collias & Collias, 1978; Collias & Collias, 2004; Lewis, 1982).

Standardized simulated territorial intrusions

Behavioural responses (of 122 individuals) to the simulated territorial intrusions (duets from non-neighbouring pairs broadcast at 27 social group territories) revealed a marginal interactive effect between group size and social status on the probability of individual contributions to the first territorial response (Table 1), and no evidence of a sex difference in individual contributions (Table 1), when analysed following a full-model approach. Model predictions show that male and female subordinates in a small group of three were 62% and 69% (respectively) more likely to contribute to first responses than those in a group of eight, while dominants were highly likely to contribute regardless of group size, and so this is likely

363 to be a biologically meaningful difference, albeit of statistically borderline significance (Fig.
364 1). Given the marginally significant *P* value and the effect size (Table 1, Fig. 1), we interpret
365 the possible biological importance of the interaction with some caution (Amrhein, Greenland,
366 & Mcshane, 2019). Of primary interest to our core question, subordinates were significantly
367 less likely to contribute to the first response than dominants, as predicted (Table 1, Fig. 1).
368 Looking at the effect of group size on each social class separately, among dominant
369 individuals the probability of contributing to the first response was unrelated to group size
370 ($\chi^2_1 = 0.35$, $P = 0.56$; data set restricted to dominants only; Fig. 1), while among subordinates,
371 the probability of contributing to the first response decreased with increasing group size ($\chi^2_1 =$
372 13.48, $P < 0.001$; data set restricted to just subordinates; Fig. 1). Furthermore, by restricting
373 the data set to only the first STI at a group, we can rule out the possibility that the results
374 from the full data set are driven by habituation or carryover effects (status*group size
375 interaction: $\chi^2_1 = 8.07$, $P = 0.005$; status: $\chi^2_1 = 32.2$, $P < 0.001$; group size: $\chi^2_1 = 7.66$, $P =$
376 0.005).
377
378 The probability of an individual subsequently contributing at any point during the response to
379 an STI was not significantly predicted by any of the fitted terms (Table 1), as the majority of
380 individuals did eventually join the response. In this case, absolute model estimate values
381 should be treated with some caution, because the model was one-inflated due to 82% of
382 individuals contributing at some point during the trial. Despite being observed as present with
383 the group during the trials, 18% of individuals (notably, exclusively subordinates) failed to
384 contribute at all. A high variance estimate for the random term bird identity in the full model
385 (365.6 ± 19.12) suggests that individuals were consistent in their responses; for those with
386 repeated measures during different STI sessions (32 individuals with 2–4 observations per
387 individual), 81% responded with the same response type (either contributing or not

388 contributing at all during the session), with only six individual birds showing variation in
389 response type across separate trials.
390
391 While it is clear that dominant individuals are especially aggressive and will forcefully repel
392 both conspecifics and heterospecifics from their territory rapidly and with great vigour (York,
393 n.d. Unpublished raw data) and engage in dominance interactions with subordinates in the
394 group (Collias & Collias, 1978; Harrison et al., 2014), there was no evidence of immediate
395 within-group punishment of individuals that did not contribute at all, or contributed less, as
396 evidenced by a lack of any observed subordinate-directed aggression during the trials.
397
398 ***Threat level experiment***
399 Data from the paired within-individual repeated measures experiment were analysed to
400 investigate whether individual contributions are adjusted in response to the level of threat
401 presented. Focusing on the dominant male and oldest subordinate male in each group, our
402 analyses revealed that both classes of male responded significantly more rapidly to the high
403 territorial threat treatment (non-neighbour duet playback) than to the low territorial threat
404 treatment (neighbour duet playback; Table 2, Fig. 2a, b). Dominant males responded more
405 rapidly than their subordinate counterparts under both treatments (Table 2, Fig. 2a, b) and
406 there was no significant interaction between treatment and status (Table 2, Fig. 2a, b),
407 indicating that both dominants and subordinates similarly 'stepped up' their responses under
408 higher threat, leaving the dominance difference maintained under both scenarios. After the
409 trial, all males took significantly longer to return to terrestrial foraging behaviour following
410 the high territorial threat treatment (non-neighbour duet playback) than following the low
411 territorial threat treatment (neighbour duet playback; Table 2, Fig. 2c, d) and dominant males
412 took consistently longer than their subordinates (Table 2, Fig. 2c, d). Again, the more

persistent response to the higher threat treatment was due to both dominant and subordinate males taking a similarly greater amount of time to return to foraging in this context, as no significant interaction between treatment and status was present (Table 2, Fig. 2c, d).

Regarding the overall group response to the threat manipulation, a significantly larger proportion of group members contributed to the first vocal chorus in response to the high-threat treatment than the low-threat treatment (GLMM: $\chi^2_1 = 16.37$, $P < 0.001$; Fig. 3a). Groups also produced significantly longer vocal choruses during the first response to the high-threat treatment than during the first response to the low-threat treatment (LMM: $\chi^2_1 = 11.26$, $P < 0.001$; Fig. 3b).

Discussion

Contributing to competition between rival groups is predicted to occur in a payoff-dependent manner with dominant individuals contributing most to territory defence, when within-group social hierarchy determines the nature of individual benefits from defending a territory (Gavrilets & Fortunato, 2014). Our results in white-browed sparrow-weavers support this prediction, as dominant individuals were significantly more likely than subordinates to contribute to the first response to simulated territorial intrusions (probably the riskiest phase; Heinsohn & Packer, 1995), responded with shorter latencies and were slower to return to foraging following such intrusions. While the majority of group members did eventually join the collective territorial response to intrusions, a small proportion of subordinate individuals failed to contribute at all and seemed to do so consistently across repeat trials. The withholding of contributions by subordinates could call into question the benefits to dominants of tolerating the presence of subordinates within their territories, which is widely assumed to play an important role in the evolution of group living (Kingma, et al., 2014).

438 However, our results also suggest that subordinates increase their contributions when they are
439 needed most: individual subordinates were more likely to contribute to the first response to a
440 territorial intrusion when in smaller groups, and subordinates responded faster (and were
441 slower to return to foraging) when faced with territorial intrusions designed to be indicative
442 of a higher level of threat. Flexibility in subordinate contributions in relation to the scale of
443 the threat could thereby help to explain the benefits of tolerating subordinates on the territory,
444 despite their unequal contributions to defence.
445
446 Public goods theory predicts that 'privileged' individuals should contribute more to the
447 cooperative defence of territory against rivals as they stand to benefit more from effective
448 territorial defence, since their contributions in territory defence can be viewed as competition
449 with their dominant counterparts in rival groups (Gavrilets & Fortunato, 2014). While the
450 higher contributions of dominants in our study may well have arisen for precisely this reason,
451 additional or alternative mechanisms could also be at play. Dominant white-browed sparrow-
452 weavers are likely to gain greater fitness benefits from territorial retention than subordinates,
453 since they monopolize reproduction (Harrison, York, Cram, Hares, & Young, 2013; Harrison,
454 York, Cram, & Young., 2013) and may also dominate competition for resources within the
455 territory. However, as more competitive individuals, dominants could also experience lower
456 costs of contributing to territorial defence (e.g. arising from a reduced risk of injury should
457 the interaction escalate to physical aggression) than subordinates, which could also explain
458 their higher contributions. Indeed, Gavrilets and Fortunato (2014) highlighted that it is the
459 status-related differences in net payoff from contributions that should lead to 'privileged'
460 individuals contributing more to collective territorial defence, which allows for the possibility
461 that status-related differences in both benefits and costs could contribute to this pattern. It is
462 also worth noting that while the use of a shared territory can be considered a public good (as

463 all group members use the resources therein and hence stand to benefit from its collective
464 defence), in reality territorial intrusions could threaten some group members' access to the
465 public good more than others. For example, in sparrow-weaver societies, while long-term
466 monitoring of territory boundaries suggests that territorial interactions among groups impact
467 territory size (and hence potentially affecting all group members, as envisaged in a standard
468 public goods scenario), such interactions also entail a threat of dominance takeover, in which
469 extragroup individuals depose and evict resident dominants (Martin-Taylor, 2018). In this
470 latter scenario, subordinates may be able to remain within the group (and hence continue to
471 use the public good) while the previous dominant is invariably evicted (Martin-Taylor, 2018).
472 Such a dominance-related difference in the extent to which outsiders threaten an individual's
473 access to the public good (i.e. more so for dominants than subordinates in this case) could
474 therefore also help to explain the higher contributions of dominants observed in this study.
475
476 Given our results that subordinates do contribute to group territory defence (albeit at lower
477 levels than dominants) and that dominants monopolize within-group reproduction, what
478 benefit(s) might subordinates accrue from contributions to defence? As envisaged in public
479 goods scenarios (see above), subordinates in this and other species are likely to gain direct
480 fitness benefits from the effective defence of the shared territory, in both the short term (e.g.
481 via benefits of residing on a familiar territory within the family unit; Ekman & Griesser,
482 2002) and the longer term (e.g. given their downstream potential to secure a breeding position
483 within the territory; Woolfenden & Fitzpatrick, 1978; Harrison et al 2014). In cooperatively
484 breeding species, such as white-browed sparrow-weavers, the vast majority of subordinate
485 individuals are offspring from previous generations that have not dispersed and hence are
486 engaging in the cooperative defence of territory alongside related dominants (typically their
487 parents; Bergmüller et al., 2007; Cockburn, 1998; Hatchwell, 2009; Lukas & Clutton-Brock,

2012). Subordinates within their natal groups may thereby also stand to gain indirect fitness benefits from defending the territory's resources (a public good) for use by relatives, and by defending the dominants themselves (and their future reproductive success) from displacement by unrelated extragroup individuals (Hatchwell, 2009). Indeed, the indirect benefits to subordinates of contributions to territorial defence are likely to be an important source of selection for the maintenance of subordinate contributions to territory defence in cooperatively breeding societies, in addition to the direct benefits that are typically the focus of public goods scenarios (Duncan et al., 2019; Gavrilets & Fortunato, 2014; Hatchwell, 2009). While we did not investigate the extent to which individual variation in inclusive fitness payoffs from investment in territorial defence explains individual variation in subordinate contributions for our focal species in this study, the lack of a sex difference in the probability that subordinates inherit the breeding position within their natal groups (Harrison et al., 2014), coupled with the likely lack of a sex difference between subordinates in the indirect benefits to be accrued from defence of the natal territory, could explain why we found no evidence here of a clear sex difference in subordinate contributions to territory defence.

Failure to contribute sufficiently to the maintenance of a public good by subordinates could be met with punishment (Bergmüller et al., 2007; Bshary & Bergmüller, 2008). Indeed, in some cooperatively breeding societies, subordinates are thought to 'pay to stay', a scenario in which the dominant's toleration of their presence within the territory is contingent upon their cooperative contributions, with failure to contribute being punished with aggressive eviction (Zöttl et al., 2013). However, we found no evidence of immediate overt punishment (via within-group behavioural aggression) in our study despite variation in subordinate contributions that could attract punitive aggression by dominants. It is conceivable, however,

513 that such aggression was delayed and therefore would not have been observed during the
514 trials. Moreover, the threat of punishment could conceivably have played a role in the
515 maintenance of cooperation at the levels observed in this study, as individual subordinates
516 could have maintained their contributions at the level required to avoid eliciting punishment
517 (Cant & Young 2013). While punishment is a frequently observed mechanism enforcing
518 cooperation in humans, it is much more rarely observed in animal societies (Raihani et al.,
519 2012; Riehl & Frederickson, 2016). It is possible that, because adaptive cheating in nature is
520 often at low frequencies in populations due to frequency-dependent selection, or because
521 uncooperative individuals experience lower fitness (Riehl & Frederickson, 2016), punishment
522 in the form of using aggression to enforce cooperation need only arise in a very limited set of
523 circumstances (e.g. in social groups in which relatedness is typically low).
524
525 Some caution is needed in the interpretation of cooperative contributions to any territorial
526 defence activities that do not involve immediate engagement in fighting with extragroup
527 individuals, as some resident members could contribute to a movement, vigilance and/or
528 vocal response not because they intend to contribute to a collective aggressive repulsion of
529 rival intruders, as is often envisaged in theoretical and empirical studies, but instead because
530 approaching, assessing or advertising to intruders could offer resident individuals other
531 benefits (e.g. if intruders constitute potential mates; Thompson & Cant, 2018). This is a
532 challenge for such studies but needs to be more widely acknowledged. Indeed, this highlights
533 a possible need for caution in interpretation of the outcomes of our territory 'threat'
534 manipulation experiment in the current study. While unfamiliar non-neighbouring pairs are
535 likely to pose a greater threat than established neighbours (because of the higher risk of
536 territory takeover), our finding of stronger territorial responses by both subordinates and
537 dominants in this context could reflect the possibility that individuals show differential

538 interest in the unfamiliar birds whose vocalizations are being presented (e.g. as potential
539 immediate or future mates). However, in our focal species, both within- and between-group
540 reproduction is monopolized by dominant individuals, and dominant males sing a separate
541 song repertoire in solo performances in sexual contexts primarily at dawn, which suggests
542 that reproductive and territorial information exchange are conducted via discrete channels in
543 this system, making an 'information-gathering' function of intergroup encounters less likely
544 to play the primary role in individual responses to territory intrusions (Collias & Collias,
545 1978; Collias & Collias, 2004; Voigt, Leitner, & Gahr, 2005; Walker et al., 2016; York,
546 2012; York et al., 2016). Furthermore, all our data were collected outside the context of
547 breeding activity for the focal groups; therefore, if any sexually selected benefits of attending
548 to information during intergroup encounters do exist, these benefits would be of low reward
549 in the context of this specific study.
550
551 Our findings suggest that subordinates contribute less to territorial defence than dominants,
552 and that their contributions appear to decrease with increases in their group size. These
553 findings highlight that while dominants may indeed accrue territorial defence benefits from
554 tolerating the presence of additional subordinates, these benefits may be more modest than is
555 generally appreciated as each subordinate contributes less as group size increases. As
556 selection for helping to rear the offspring of dominants is also frequently thought to arise in
557 part from direct benefits to helpers resulting from the territorial gains to be accrued from
558 rearing more group members (the group augmentation hypothesis; Woolfenden & Fitzpatrick,
559 1978; Kingma et al., 2014), the benefits of helping behaviour that arise through this
560 mechanism could also be more modest than is generally recognized. However, our findings
561 do also suggest that subordinates increase their contributions when they are needed most, and
562 this context dependence might thereby underpin the territorial benefits to be accrued from

563 additional subordinates, perhaps particularly so when faced with larger opposition groups
564 (Packer, Scheel, & Pusey, 2002). While all simulated territorial intrusions in this study
565 involved the playback of duets recorded from a breeding pair (simulating an intruder group
566 size of two), note that white-browed sparrow-weaver groups range from two to 12
567 individuals, and larger groups have larger territories and appear to outcompete neighbours for
568 space (Martin-Taylor, 2018). Consequently, it is possible that subordinates in large groups
569 (which were unlikely to contribute to the first territorial response in our study, when faced
570 with a simulated intrusion by a pair; Fig. 1) would increase their contributions when faced
571 with intrusions by numerically larger opponents, if neighbouring resident groups compete
572 directly over territory and larger groups reflect a more significant threat to their territory.
573 Investigating this possibility, and its implications for the patterns of selection that arise from
574 intergroup conflict, may provide an avenue for future research.
575
576 We do not yet know the extent to which individual contributions to cooperative territory
577 defence in white-browed sparrow-weavers are individually consistent, although our results do
578 suggest that they may be consistent under the same context, but express flexibility between
579 different contexts. Consistent individual differences in subordinate white-browed sparrow-
580 weavers could underlie different classes of 'contributor' phenotypes and thereby explain the
581 presence of individuals that never contributed to group territory defence in the context of
582 simulated territory intrusions. For example, cooperatively nesting greater ani, *Crotophaga*
583 *major*, appear to have two types of consistent cooperative strategies in the context of
584 communal nesting: either never cheat ('pure cooperative' strategy) or cooperate and cheat
585 ('mixed' strategy), which demonstrates that cooperation and cheating can coexist stably in
586 the same population via individual tactics (Riehl & Strong, 2019). Similarly, female lions
587 (*Panthero leo*) exhibit individual differences in their contributions to group territory defence

(Heinsohn & Packer, 1995) and cooperatively breeding meerkats, *Suricata suricatta*, and banded mongooses, *Mungos mungo*, show consistent individual differences in offspring care (English, Nakagawa, & Clutton-Brock, 2010; Sanderson et al., 2015).

In summary, our findings contribute to a wider body of evidence suggesting that dominants frequently contribute more to territorial defence than subordinates and in so doing are consistent with, and hence lend support to, the predictions of economic theory that privileged individuals contribute more. Where subordinates contribute less, our findings suggest that they may nevertheless step up when needed most, and this plasticity may in part underpin their continued toleration by dominants.

Author Contributions

J.E.Y. and A.J.Y. conceived and designed the study. J.E.Y. and K.J.W. performed field data collection. J.E.Y. conducted data analysis. J.E.Y. and A.J.Y. wrote the manuscript.

Data Availability

Data are available at the Mendeley repository: http://dx.doi.org/10.17632/trb75pkfyk.1

Declaration of Interest

We declare no conflict of interest.

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Table 1

Individual contributions to simulated territorial intrusions

Response term	Explanatory terms	Estimate ± SE	χ^2	*P*
Probability of contributing during first response (Yes/No)	Status: subordinate	0.34 ± 2.16	40.09	<0.001
	Group size	-0.01 ± 0.36	0.00	1.00
	Sex: male	-0.40 ± 0.70	0.42	0.517
	Group size*status	-0.85 ± 0.63	3.77	0.052
	(Intercept)	3.22 ± 2.12		
	Bird ID	2.76 ± 1.66		
Probability of contributing during trial (Yes/No)	Status: subordinate	7.08 ± 10.86	0.82	0.37
	Group size	1.87 ± 3.10	0.21	0.64
	Sex: male	-0.09 ± 1.82	0.003	0.96
	Group size*status	-2.30 ± 3.18	1.01	0.31
	(Intercept)	4.12 ± 9.72		
	Bird ID	365.6 ± 19.12		

The *P* value for each term is based on the chi-square test (likelihood ratio test) for change in deviance when comparing models with or without that term (given the borderline significance of the Group size*status interaction, we also report the χ^2 and *P* values for the Status and Group size terms in isolation, following removal of the interaction, to aid interpretation). The mean estimates ± SE are reported for all terms in the full model. GLMM: generalized linear mixed-effects model. GLMM estimates are raw values from model (logit-link function). Variance and SD are reported for the random term Bird ID.

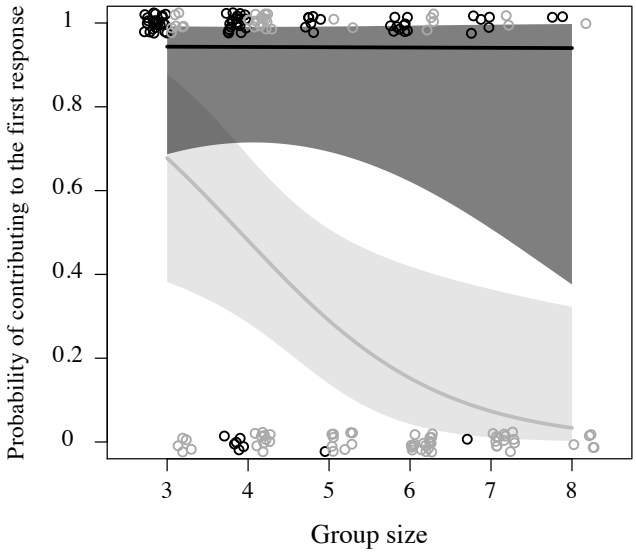
Table 2

Dominant and subordinate male responses to experimental manipulation of the scale of the territory threat

Response term	Explanatory terms	Estimate ± SE	χ^2	*P*
Latency to first response	Treatment*status	1.06 ± 0.98	1.34	0.25
	Treatment: non-neighbour	2.08 ± 0.60	29.69	<0.001
	Status: subordinate	-2.08 ± 0.85	9.96	0.002
	Bird ID	<0.001 ± 0.020		
	Group	1.78 ± 1.33		
Latency to resume foraging	Treatment*status	-0.30 ± 0.66	0.19	0.66
	Treatment: non-neighbour	-0.59 ± 0.47	5.45	0.02
	Status: subordinate	1.06 ± 0.47	6.80	0.009
	Bird ID	<0.001 ± 0.019		
	Group	0.32 ± 0.57		

The *P* value for each term is based on the chi-square test (likelihood ratio test) for change in deviance when comparing models with or without that term. The mean estimates ± SE are reported for all terms in the full model. Variance and SD are reported for the random terms Bird ID and Group.

825



826

827 **Figure 1.** Individual contributions to simulated territorial intrusions in relation to social status
828 and group size. The probability of white-browed sparrow-weaver (dominants: black circles;
829 subordinates: grey circles) contributions to group territory defence, in relation to group size
830 (lines show predicted probabilities of responding and grey shading represents 95%
831 confidence intervals from a GLMM with the variables of group size, social status and their
832 interaction as fixed effects, and bird identity fitted as a random term).

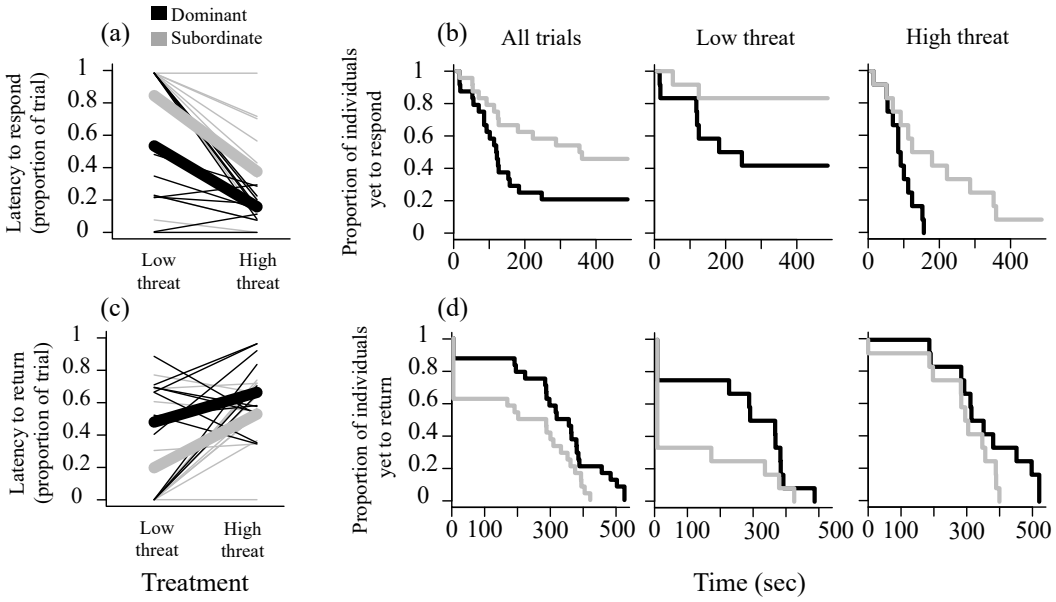
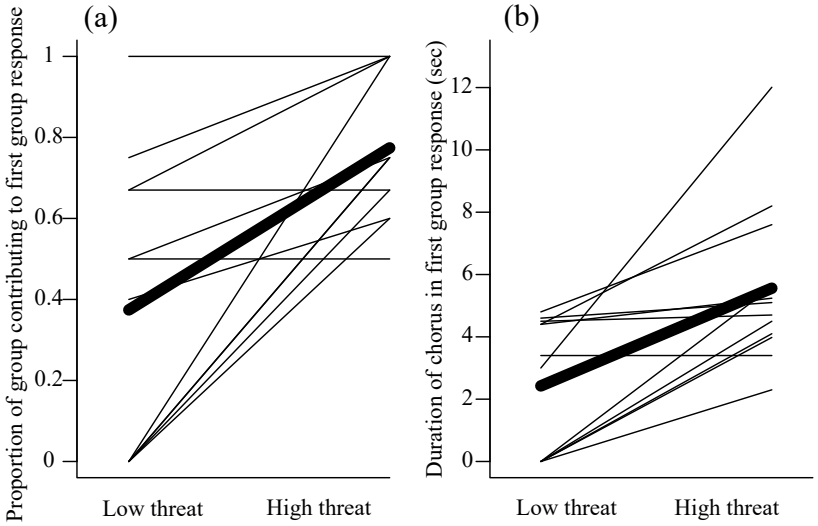


Figure 2. Dominant and subordinate male responses to experimental manipulation of the scale of the territory threat. (a) Paired data (thicker bars represent raw mean) showing latency to the first response from each dominant (black) and subordinate (grey) male during simulated intrusion of high threat (non-neighbour duet) or low threat (neighbour duet). (b) Proportion of focal males (dominants: black; subordinates: grey) yet to show their first response across the observation period (3 min playback trial followed by 5 min post-playback observation) displayed for all trials, low-threat playbacks and high-threat playbacks. (c) Paired data (thicker bars represent raw mean) showing latency to resume foraging for each dominant (black) and subordinate (grey) male during simulated intrusion of high threat (non-neighbour duet) or low threat (neighbour duet). (d) Proportion of focal males (dominants: black; subordinates: grey) yet to resume foraging during the observation period displayed for all trials, low-threat playbacks and high-threat playbacks.



846

847 **Figure 3.** Overall group responses to experimental manipulation of the scale of the territory
848 threat. Paired contrasts of (a) the proportion of the group contributing to the first vocal chorus
849 response and (b) vocal chorus duration, under low and high threat. Means are shown as a
850 thicker black line.

851